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Algae community response to climate change and nutrient loading recorded by sedimentary phytoplankton pigments in the Changtan Reservoir, China

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ABSTRACT

Climate change is likely to stimulate variations in phytoplankton composition and production in gradually eutrophicating water, with negative consequences for the water quality of many reservoirs. This study analyzed the effects of climate warming and increased nutrient loading on algae communities recorded by sedimentary pigments in the Changtan Reservoir of southeastern China from 1985 to 2015. Pigment profiles indicated that cyanobacteria, green algae, diatoms, and cryptophytes were the dominant algae groups during the study period. Algae biomass increased significantly after 2007, correlated (by the Mann-Kendall test) with an upswing in nutrient load and rising air temperatures. Generalized additive model (GAM) analysis demonstrated that total phosphorous was the dominant contributor to algae biomass during the study period, accounting for 41.37%, 43.86%, 58.91%, 97.36%, and 70.24% of variations in total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass, respectively. The relative contributions of annual average air temperature to variations in total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass were 10.80%, 14.02%, 14.13%, 24.64%, and 17.31%, respectively, depending strongly on nutrient load. In conclusion, climate warming and increasing anthropogenic nutrient loading forced phytoplankton dynamics and drove increasing algae biomass in this reservoir, suggesting that future water quality management practices should consider both meteorological and anthropogenic factors affecting algae communities.

1. Introduction

Climate change has increased the susceptibility of large temperate-latitude reservoirs to deterioration in the water quality due to increasing water temperature and nutrient runoff (Capo et al., 2017; Toride et al., 2018). Temperature is a crucial factor influencing phytoplankton growth and harmful algae bloom dynamics, with warming weather favoring algae bloom formation and expansions (Jiménez et al., 2015; Capo et al., 2017). In particular, heating of the epilimnion, reduced water turnover, and increasing nutrient load strongly influence the phytoplankton community and its biomass (Zhou et al., 2016), and accelerate the occurrence and risk of harmful algae blooms in such reservoirs (Yang et al., 2016). The latter are of great societal concern, as harmful algae can endanger drinking water resources, fisheries, and irrigation practices (Visser et al., 2016). Understanding the effects of climate change and human-induced modifications on historical algae communities in reservoirs is crucial to mitigating future algal blooms and protecting water resources (Yang et al., 2016).

In the absence of long-term hydro-ecological monitoring data, biomarkers from reservoir sediment cores can provide a long-term perspective regarding phytoplankton community structure succession (Deshpande et al., 2014; Waters et al., 2005). Fossil algae pigments, preserved over a long period beneath anoxic sediment, can be used as a biomarker to reconstruct historical phytoplankton populations (Szymczak-Żyła et al., 2016; Tse et al., 2015). Previous fossil pigment studies have been carried out on lake and coastal sediments to track phytoplankton community dynamics (Szymczak-Żyła et al., 2016; Waters et al., 2005), identify ecologically significant events over historical time scales (Reuss et al., 2005; Romero-Viana et al., 2010) and/or determine past cyanobacterial episodes (Deshpande et al., 2014). Relatively little research has focused on the accumulation of sedimentary pigments in artificial reservoirs, despite the stable and undisturbed hydrologic conditions conducive to pigment preservation (Tse et al., 2015).

Recent studies have confirmed the interactive impacts of climate change and human activities on phytoplankton composition and productivity (O'Beirne et al., 2017; Zhou et al., 2016). However, few researchers have clearly and quantitatively explained the contributions of

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climate change and human activities to changes in phytoplankton communities over long time periods (Mwangi et al., 2016). As the relationships between climate change and anthropogenic activities are controlled through complex interactions (Marieke et al., 2013), significant knowledge gaps remain regarding how to separate and quantify their impacts (Visser et al., 2016). Distinguishing between the impacts of climate change and human activities can be achieved through empirically-based and/or processing-based methods (Mwangi et al., 2016). For example, generalized additive modeling (GAM), a processing-based non-parametric method, was recently used to separate the contributions of nutrient enrichment and climate warming on variations in microbial eukaryotic diversity in two deep lakes within the French Alps (Capo et al., 2017).

It is hypothesized that climate change and human activities have a synergistic effect on phytoplankton communities and biomass, and we designed this study to: (1) estimate the preservation condition of fossil pigments by applying stable derivatives and a degradation index, (2) determine historical phytoplankton production and communities, and (3) use GAMs to quantify the impact of climate change and anthropogenic activities on phytoplankton biomass.

2. Materials and methods

2.1. Study area and sediment sampling

The Changtan Reservoir (N 28°30′–28°40′, E 121°00′–121°04′), located in Taizhou City, southeastern China (Fig. 1), was built at 1964 with a water area of 35.5 km^2, a mean depth of ca 12 m and a catchment area of 514 km^2. The catchment is influenced by a subtropical monsoon climate, with an annual average temperature of 17 °C and annual average rainfall of 1874.8 mm. The reservoir plays an important role in regional socioeconomic development by providing drinking water supply, flood control, irrigation, and electricity generation. However, it has become mesotrophic due to increasing nitrogen and phosphorus inputs from agricultural fertilizer and livestock farming.

Two sediment cores (CT-0 and CT-8) were collected from different locations within the reservoir using a gravity columnar sediment sampler (8 cm in diameter, 60 cm length) in March 2017 (Fig. 1). The sampling sites were chosen away from reservoir banks, stream inlets and the reservoir outlet to diminish any disturbance of the sediment by scouring or re-suspension. The cores were immediately subsampled at 1 cm intervals and transported to a laboratory in an ice-filled cooler. All samples were freeze-dried in an FD-1A-50 freeze dryer and ground through 100 mesh screens, then stored in the dark at −80 °C.

2.2. Sample analysis

Homogenized freeze-dried sediment (~1 g) was extracted in 3 ml acetone-water mixture (95: 5 v: v). The mixture was sonicated in an ice-water bath for 15 min and filtered through a 0.45 μm PTFE filter. All extracts were stored in the dark at −80 °C until analysis. An Agilent 1200 series high-performance liquid chromatograph (HPLC) equipped with a diode-array detector (Agilent Technologies Inc., Palo Alto, CA, USA) was used for pigment analysis. A Waters Symmetry C8 column (150 × 4.6 mm, 3 μm) was used for separation (Jiang et al., 2017). Commercially available external standards from DHI Inc. (Hørsholm, Denmark) were used for peak identification and quantification of 19 pigment types: chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll *c2* (Chl *c2*), pheophytin *a* (Phe *a*), pheophorbide *a*, (Pheide *a*), Mg-2,4-divinylpheoporphyrin (MgDVP), alloxanthin (Allo), canthaxanthin (Cantha), β,β-carotene (ββ-Car), diadinoxanthin (Diadino), diatoxanthin (Diato), fucoxanthin (Fuco), 19′-hex-fucoxanthin (Hex-Fuco), lutein (Lut), neoxanthin (Neo), peridinin (Peri), prasinoxanthin (Pras), violaxanthin (Viola), and zeaxanthin (Zea).

2.3. ^{210}Pb dating

The sediment cores were dated by using ^{210}Pb techniques (Zan et al., 2012), performed by γ ray spectrometry (ORTEC, USA) on a DSPEC jr 2.0 multi-channel spectrometer. ^{210}Pb and ^{226}Ra activity in sediment samples was determined by γ rays emitted at 46.5 keV and 352 keV, respectively. Excess ^{210}Pb ($^{210}Pb_{ex}$) activity was obtained by ^{226}Ra activity from total ^{210}Pb activity using the constant rate of supply (CRS) dating model. The standard sample of ^{210}Pb was supplied by the Institute of Atomic Energy, Chinese Academy of Sciences. The average sediment accumulation rate at cores was 0.0451 g cm^{-2} y^{-1}.

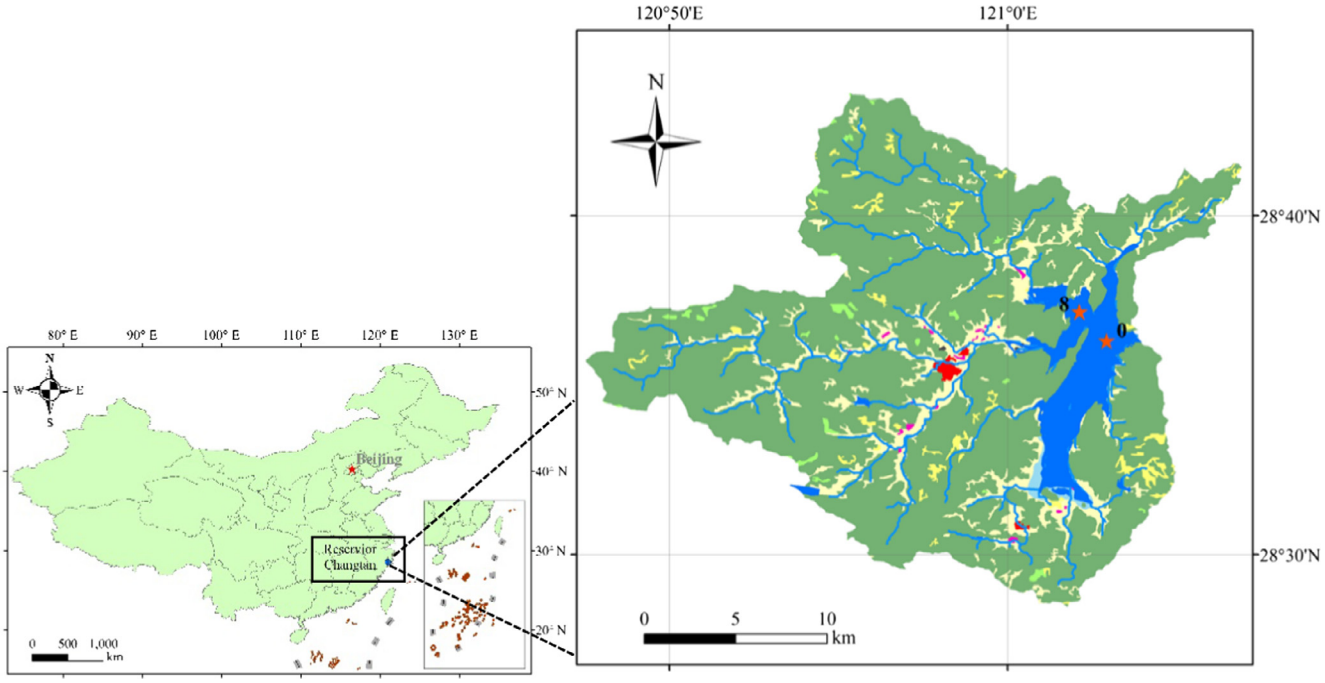

Fig. 1. Location of study area and sampling sites.

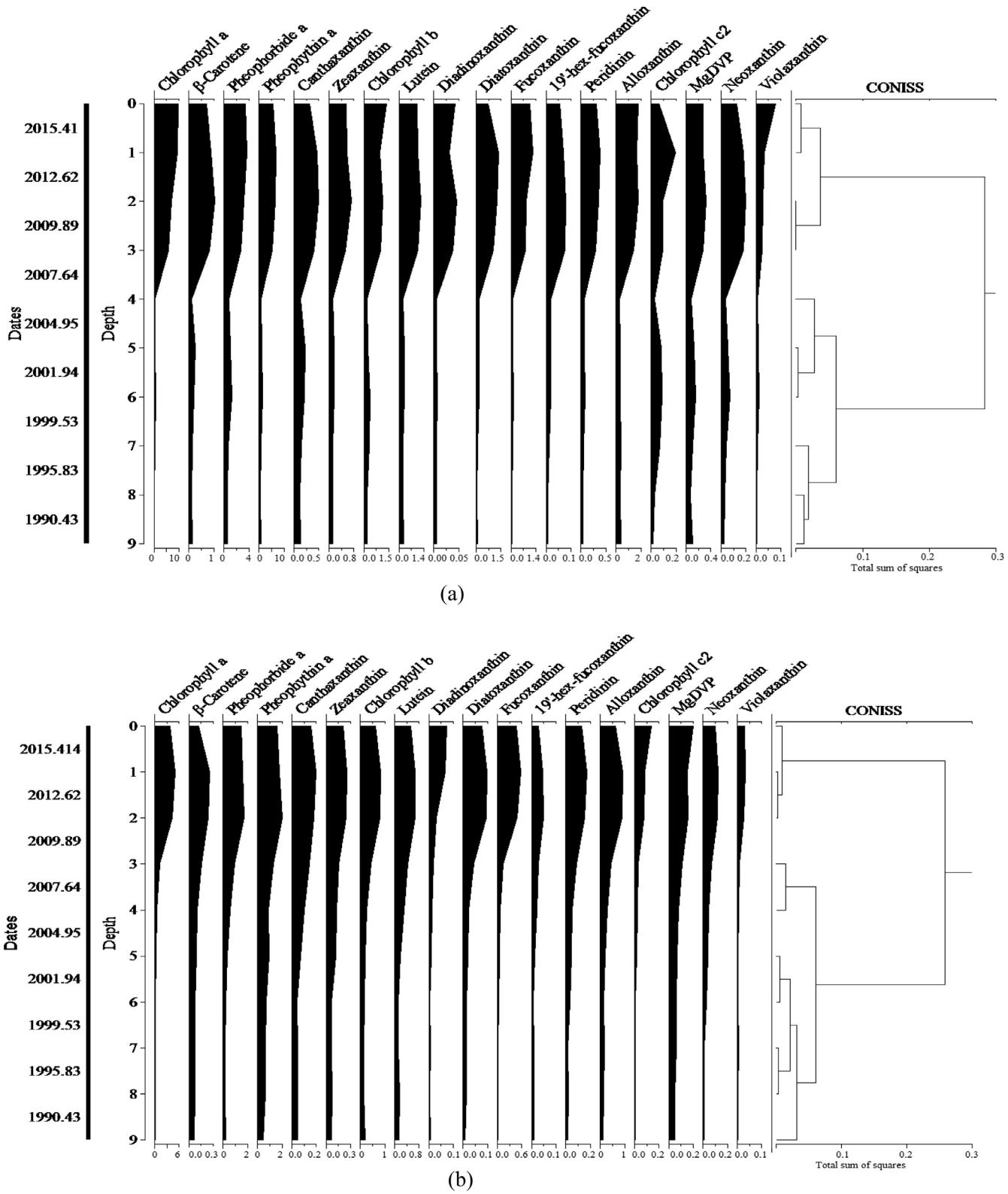

Fig. 2. Profiles of phytoplankton pigments from core samples CT-0 (a) and CT-8 (b). All compounds are expressed as μg pigment g^{-1} sediment.

2.4. Data processing

Pigment concentration profiles were developed with TILIA v.2.0.41 software, which used Constrained Incremental Sums of Squares Cluster Analysis (CONISS) for the constrained cluster analysis. Correlations between sedimentary pigments and nutrients or meteorological factors were analyzed by Spearman correlation coefficient (SPSS system v16.0). OriginPro 8 and SigmaPlot 9.0 were used for plotting the figures.

Meteorological data were derived from the CN05.1 grid observation dataset, which was constructed by the anomaly approach during interpolation with a horizontal resolution of 0.25° × 0.25° (Xu et al.,

Table 1
Spearman-Rho-correlations of sedimentary pigments, sedimentary nutrients (LOI, TN, TP) and meteorological factors of CT-0 and CT-8.

	HexFuco	Allo	Cantha	Chla	Chlb	Chlc2	Diadino	Diato	Fuco	Lut	MgDVP	Neo	Peri	Pheidea	Phea	Viola	Zea	ββ-Car	LOI	TN	TP	Tem	Tmax	Pre
HexFuco	1																							
Allo	0.790**	1																						
Cantha	0.860**	0.930**	1																					
Chla	0.949**	0.733**	0.781**	1																				
Chlb	0.910**	0.905**	0.903**	0.877**	1																			
Chlc2	0.843**	0.885**	0.935**	0.800**	0.920**	1																		
Diadino	0.814**	0.712**	0.703**	0.765**	0.845**	0.685**	1																	
Diato	0.911**	0.906**	0.949**	0.881**	0.920**	0.900**	0.787**	1																
Fuco	0.911**	0.906**	0.947**	0.886**	0.968**	0.950**	0.794**	0.971**	1															
Lut	0.893**	0.907**	0.932**	0.855**	0.918**	0.876**	0.767**	0.939**	0.942**	1														
MgDVP	0.826**	0.948**	0.970**	0.781**	0.926**	0.942**	0.739**	0.952**	0.963**	0.935**	1													
Neo	0.924**	0.885**	0.923**	0.889**	0.960**	0.929**	0.817**	0.968**	0.983**	0.927**	0.941**	1												
Peri	0.894**	0.889**	0.927**	0.897**	0.936**	0.912**	0.752**	0.966**	0.980**	0.964**	0.949**	0.965**	1											
Pheidea	0.883**	0.921**	0.965**	0.840**	0.953**	0.958**	0.750**	0.945**	0.983**	0.952**	0.973**	0.952**	0.964**	1										
Phea	0.852**	0.767**	0.823**	0.889**	0.844**	0.774**	0.783**	0.928**	0.895**	0.838**	0.854**	0.903**	0.907**	0.840**	1									
Viola	0.876**	0.829**	0.874**	0.872**	0.856**	0.874**	0.747**	0.939**	0.913**	0.824**	0.879**	0.915**	0.878**	0.875**	0.908**	1								
Zea	0.891**	0.905**	0.934**	0.859**	0.914**	0.882**	0.770**	0.954**	0.943**	0.981**	0.936**	0.940**	0.966**	0.936**	0.874**	0.846**	1							
ββ-Car	0.814**	0.931**	0.972**	0.772**	0.883**	0.920**	0.622**	0.930**	0.934**	0.927**	0.964**	0.912**	0.940**	0.951**	0.823**	0.846**	0.939**	1						
LOI	0.619**	0.869**	0.838**	0.593**	0.787**	0.850**	0.568**	0.733**	0.797**	0.801**	0.875**	0.735**	0.779**	0.870**	0.604**	0.675**	0.769**	0.846**	1					
TN	0.793**	0.648**	0.618**	0.857**	0.806**	0.665**	0.834**	0.708**	0.732**	0.704**	0.655**	0.737**	0.715**	0.692**	0.782**	0.742**	0.717**	0.586**	0.577**	1				
TP	0.782**	0.825**	0.890**	0.772**	0.833**	0.857**	0.624**	0.865**	0.893**	0.864**	0.887**	0.848**	0.905**	0.909**	0.780**	0.756**	0.872**	0.905**	0.819**	0.562**	1			
Tem	0.491**	0.289*	0.391**	0.534**	0.437**	0.404**	0.374**	0.501**	0.508**	0.417**	0.401**	0.543**	0.511**	0.412**	0.580**	0.522**	0.464**	0.413**	0.105	0.329**	0.373**	1		
Tmax	0.595**	0.430**	0.447**	0.593**	0.492**	0.398**	0.468**	0.547**	0.533**	0.559**	0.448**	0.550**	0.565**	0.497**	0.540**	0.501**	0.556**	0.444**	0.274*	0.413**	0.456**	0.435**	1	
Pre	0.004	0.038	−0.005	0.058	0.001	0.063	−0.025	0.007	0.016	0.040	0.013	0.018	0.037	0.039	−0.015	0.058	0.019	0.016	0.093	0.047	0.045	−0.008	0.012	1

* Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).

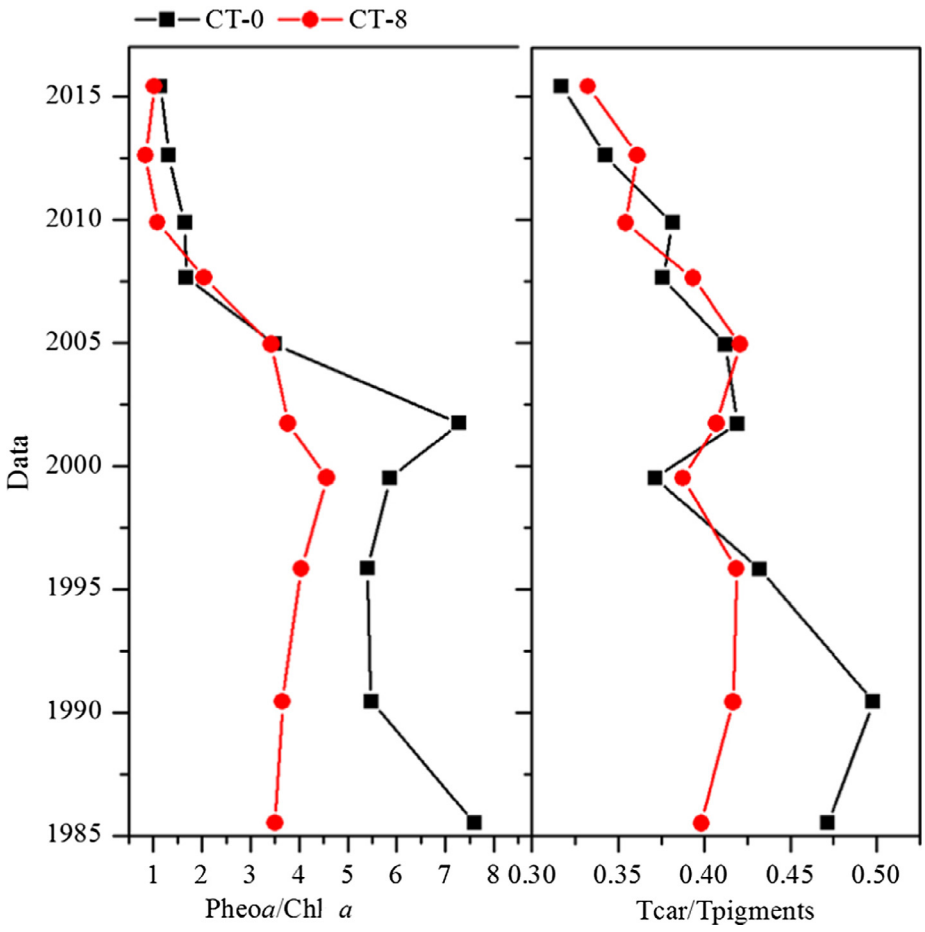

Fig. 3. Indicators of degradation in sediments at the two coring sites.

2009). The non-parametric Mann-Kendall (M-K) statistical test, performed in Matlab software (R2014a), was used to assess the presence of monotonic upward or downward trends in meteorological factors over time (Toride et al., 2018).

In this case, the null hypothesis meant that no significant monotonic trends were present. Given a meteorological factor time series $x = \{x_1, x_2, \ldots, x_n\}$, the M-K test statistic S is given by:

$$S = \sum_{i}^{n-1} \sum_{j=i+1}^{n} \mathrm{sgn}(x_j - x_i) \tag{1}$$

where sgn $(x_j - x_k)$ is the sign function of $x_j - x_k$. The variance of S is calculated as:

$$\mathrm{var}(S) = \frac{n(n-1)(2n+5) - \sum_{i-1}^{m} t_i(t_i-1)(2t_i+5)}{18} \tag{2}$$

where m is the number of tied groups and t_i is the number of observations in the ith tied group. Then the normalized statistic is given by:

$$Z = \begin{cases} \frac{S+1}{\sqrt{\mathrm{var}(S)}}, & if\ S < 0 \\ 0, & if\ S = 0 \\ \frac{S-1}{\sqrt{\mathrm{var}(S)}}, & if\ S > 0 \end{cases} \tag{3}$$

The null hypothesis would be rejected if the absolute value of Z exceeded 1.96 with $\alpha = 0.05$, and vice versa. More details on this methodology are given in Toride et al. (2018).

GAM analysis is suitable for analysis the impact of human activities and climate change on algae biomass (Capo et al., 2017). GAMs are nonparametric regression models driven by data rather than predetermined by a priori models. GAM analysis is an effective method because it can directly assess the nonlinear relationship between a response variable and multiple explanatory variables without any restrictive assumptions. The method's general structure is given by:

$$g(\mu) = \beta_0 + \sum_{i=1}^{k} s_i(x_i) + \varepsilon \tag{4}$$

where μ is the response variable, β_0 is a constant intercept term, $s_i(x_i)$ is the unknown smooth function of explanatory variable x_i, and ε is the residual.

The Akaike information criterion (AIC) and generalized cross validation (GCV) score were used to select the predictors and decide on their inclusion in or exclusion from the model (Mosammam et al., 2016). Smaller AIC values indicated that the model could explain more information with less complexity than a model with larger AIC values. The GCV criterion was applied to automatically select the parameters of smooth functions with an iterative approach, improving the calculation efficiency and helping to determine whether the GCV score decreased when one variable was removed (Song et al., 2015; Wood, 2017). The sedimentary total phosphorus (Sed-TP) and annual average air temperature (Tem) were selected as representative predictor variables, while the response variables included the concentrations of sedimentary ββ-Car, Zea, Lut, Diadino, and Allo, indicating variations in total algae, cyanobacteria, green algae, diatoms, and cryptophytes, respectively. All five GAM analyses used the "mgcv" package in R.

3. Results and discussion

3.1. Pigment preservation and profile distribution

Sedimentary pigments were influenced by photo and chemical oxidation, as well as herbivore grazing pressure, before entering the fossil record (Reuss et al., 2005). Therefore, the absolute concentration of fossil pigments as a credible record of primary productivity depends on how well the pigment is preserved (Deshpande et al., 2014; Tse et al., 2015). Highly labile pigments, such as the ubiquitous Chl *a* and Fuco (diatoms), were detected well above limited concentrations (Fig. 2), indicating weak diagenetic processes occurring within the collected cores. In addition, Pheide *a* and Phe *a*, the dominant and most stable Chl *a* degradations, can provide insight regarding syn-depositional and post-depositional environment conditions of sedimentary pigments (Szymczak-Żyła et al., 2016). The significant correlation between Chl *a* and Phe *a* in the Changtan Reservoir ($r = 0.844$, $n = 62$, $p < 0.01$; Table 1) shows that the effect of diagenetic processes on Chl *a* should be weak, as a small fraction of Chl *a* degraded to Phe *a* in anoxic-hypoxic environment. In addition, good pigment preservation was indicated by a low ratio of pheopigment-*a* (the sum of Pheide *a* and Phe *a*) to Chl *a* (Pheo *a*/Chl *a*); this ranged from 1.14–7.60 in CT-0 and 0.84–4.56 at CT-8 sites (Fig. 3). The average Pheo *a*/Chl *a* ratios at CT-0 and CT-8 were 4.09 and 2.79, respectively, suggesting that preservation conditions were better at CT-8 than CT-0.

The ratio of total carotenoid to total identified pigments (Tcar/Tpigments) was used as an indicator of pigment degradation in sediment (Reuss et al., 2005); this ranged from 0.32–0.50 at CT-0 and 0.33–0.42 at CT-8 (Fig. 3). There was no significant trend in this ratio throughout the core, indicating that all sediments underwent the same degradation conditions (Szymczak-Żyła et al., 2016). Overall, the sedimentary pigments were preserved adequately enough for us to track the past primary productivity and phytoplankton succession as interpreted from reliable pigment trends.

All 18 photosynthetic pigment concentrations in sediment cores varied little before the mid-2000s, but increased substantially afterward (Fig. 2), which can be attributed to changes in trophic state and primary productivity (Romero-Viana et al., 2010). The CONISS results showed that the greatest difference was observed in core levels before and after the mid-2000s at both sites (Fig. 2). The Chl *a* concentration increased from 0.39 ± 0.15 (mean ± standard deviation) and 0.31 ± 0.12 μg pigment g^{-1} sediment in the first stage to 7.96 ± 1.85 and 3.58 ± 1.59 μg pigment g^{-1} sediment in the second stage at CT-0 and CT-8, respectively. ββ-Car, a better proxy for total algae biomass (Szymczak-Żyła et al., 2016), increased from 0.16 ± 0.05 and 0.07 ± 0.01 μg pigment g^{-1} sediment in the first stage to 0.86 ± 0.14 and 0.19 ± 0.06 μg pigment g^{-1} sediment in the second stage at CT-0 and CT-8, respectively. The Chl *a* and ββ-Car stratigraphy in the sediment cores demonstrated an overall increase in phytoplankton biomass in the past 30 years within two distinct periods.

3.2. Influence of anthropogenic activities on the phytoplankton community

The specific pigment content of the two sediment cores consistently represented the dominant algae community in the Changtan Reservoir (Fig. 2). The most abundant specific pigments were Cantha and Zea (from cyanobacteria), Chl b and Lutein (from green algae), Diadino, Diato, and Fuco (mainly from diatoms), Peri and Hex-Fuco (from dinoflagellates), and Allo (from cryptophytes) (Jiménez et al., 2015). Less abundant pigments included Chl c2 (minor pigment in red algae), MgDVP (from prasinoxanthin-containing algae), Neo (from mesostigmatophytes), and Viola (from chrysophytes and mesostigmatophytes) (Roy et al., 2011). There were significant correlations between many of the pigments, including between Cantha and Zea ($r = 0.934$, $n = 62$, $p < 0.01$; Table 1), Chl b and Lutein ($r = 0.918$, $n = 62$, $p < 0.01$), and Peri and Hex-Fuco ($r = 0.894$, $n = 62$, $p < 0.01$), consistent with their known co-occurrence in specific algae groups (Jiménez et al., 2015; Romero-Viana et al., 2010).

The presence of specific phytoplankton pigments throughout the stratigraphic profile indicated that cyanobacteria, green algae, diatoms, and cryptophytes were the dominating algae groups in the Changtan Reservoir over the past 30 years. Plankton sampling in 2016 and 2017 from our current work showed that the proportion of cyanobacteria was the largest, 33.72–82.47%, based on the percentage of phytoplankton abundance in each season. The percentages of green algae, diatoms, and cryptophytes were 8.42–19.23%, 7.57–39.31%, and 0.60–15.09%, respectively. Thus, the dominant algae community inferred from sedimentary pigments was consistent with the current algae monitoring data. Moreover, the 2016 and 2017 monitoring data showed that cyanobacteria were the dominant group in summer and autumn (82.47% and 74.89%, respectively), providing the potential source for algae blooms.

Nitrogen (N), P, and N: P ratios in the waterbody are vital elements limiting phytoplankton growth and the principal force driving algae bloom formation (Szymczak-Żyła et al., 2016; Zhou et al., 2016). From 1985 to 2015, the sedimentary TN, TP, and N:P ratios increased markedly in the Changtan Reservoir. Previous studies have shown that increased N: P ratios created P-limiting conditions for phytoplankton and favored non-N_2-fixing cyanobacterium (Posch et al., 2012; Zhou et al., 2016). Spearman correlation analysis of our results indicated that sedimentary nutrient content (TN and TP) had a statistically strong influence on all pigment concentrations ($p < 0.01$; Table 1).

Nonpoint-source pollution was the main source of N and P input into the Changtan Reservoir, including surface runoff and discharge from crop and livestock production. The total TN emission from point source and non-point source is 41.34 t/a and 524.31 t/a respectively, the total TP emission from point source and non-point source is 8.89 t/a and 90.80 t/a respectively. Among the non-point source TN emissions, the loss of TN from urban surface runoff was 98.76 t, that from farmland runoff was 127.42 t/a, and that from livestock and poultry was 176.90 t/a. Among the TP emissions, the loss of TP from urban surface runoff was 4.48 t, that from farmland runoff was 2.81 t/a, and that from livestock and poultry was 64.13 t/a. The significant upsurge in algae biomass in the reservoir since the mid-2000s was associated with anthropogenic activities such as increasing agriculture and industrialization, as well as urbanization in Taizhou City. Concurrently, a serious cyanobacterial bloom occurred over hundreds of square kilometers in the middle and lower reaches of the Yangtze River basin in May 2007 (Yang et al., 2016). It is noteworthy that nutrients play an important role in phytoplankton biomass increases and algae bloom formation (Jiménez et al., 2015; Zhou et al., 2016), while climate change (e.g., warming) favors the expansion of algae blooms directly or indirectly (Capo et al., 2017; Yang et al., 2016).

3.3. Impacts of meteorological factors on the phytoplankton community

Significant variations in temperature and annual maximum air temperature (T_{max}) were observed during the past ~30 years at the Changtan Reservoir ($p < 0.05$). temperature, T_{max}, and precipitation increased by 1.31 °C, 2.35 °C, and 8.36 mm, respectively, from 1985 to 2016 (Fig. 4a–c). The M-K test results showed that the progressive rank series of temperature and T_{max} increased and surpassed the 0.05 confidence level, indicating that the temperature and T_{max} had a statistically significant upward trend from 1985 to 2016 (Fig. 4d, e). However, the progressive and retrograde rank series of precipitation exhibited no significant trend over the past 30 years (Fig. 4f). Potential trend turning points were estimated when the progressive and retrograde rank series intersected in the confidence interval (Toride et al., 2018), suggesting that the increasing trend of temperature and T_{max} transited to a stable condition around 1997 and 2003, respectively.

Significantly positive correlations were found between sedimentary pigments and both temperature and T_{max} at the Changtan Reservoir

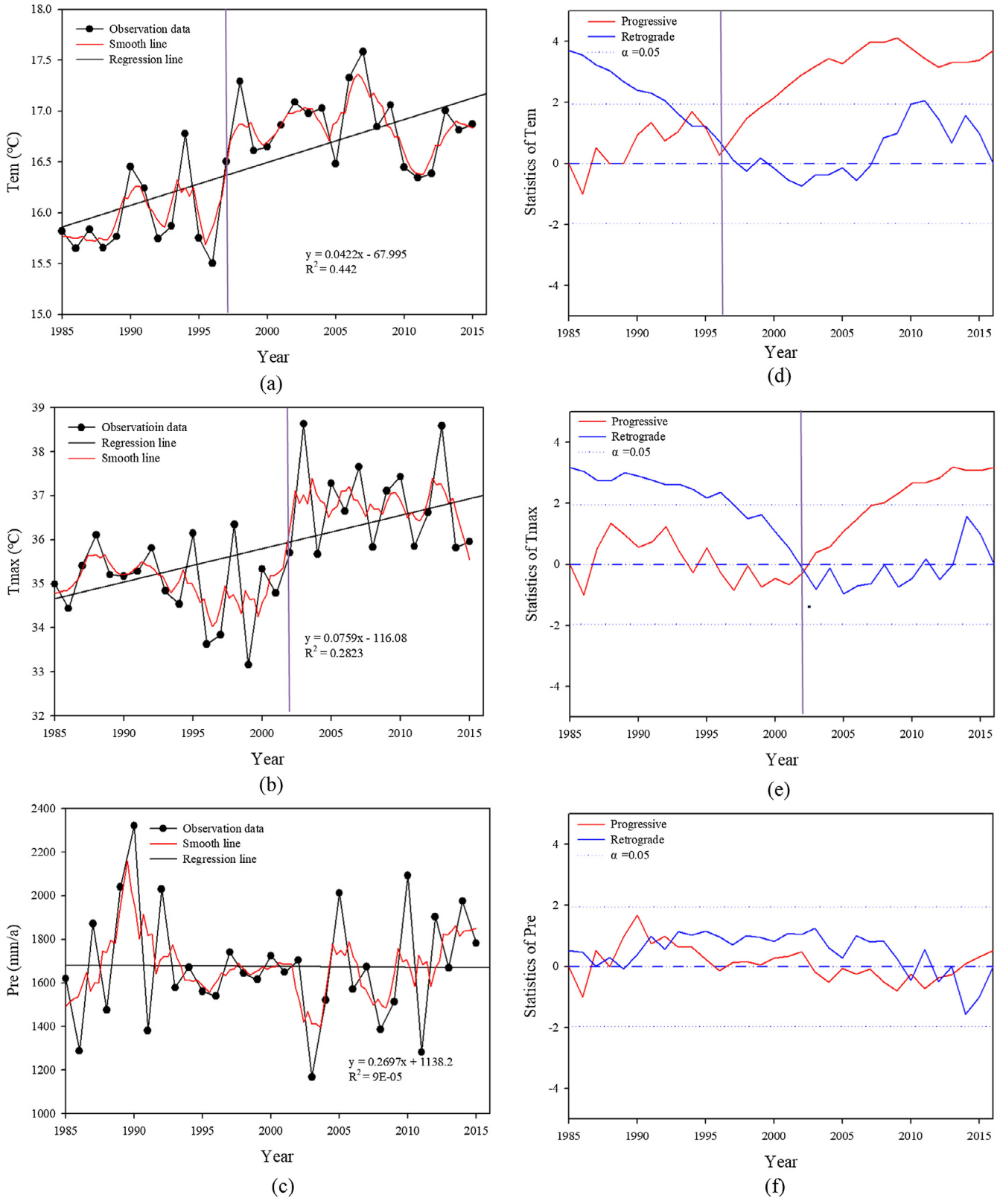

Fig. 4. Analysis of meteorological factors showing time series of reconstructed (a) annual average air temperature (Tem), (b) annual maximum air temperature (Tmax), and (c) annual precipitation (Pre) at the Changtan Reservoir. Sequential Mann-Kendall statistical test results are given for (d) Tem, (e) Tmax, (f) Pre. Red and blue lines show the progressive and retrograde rank series, respectively. Vertical purple lines indicate the transition periods estimated by the M-K test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

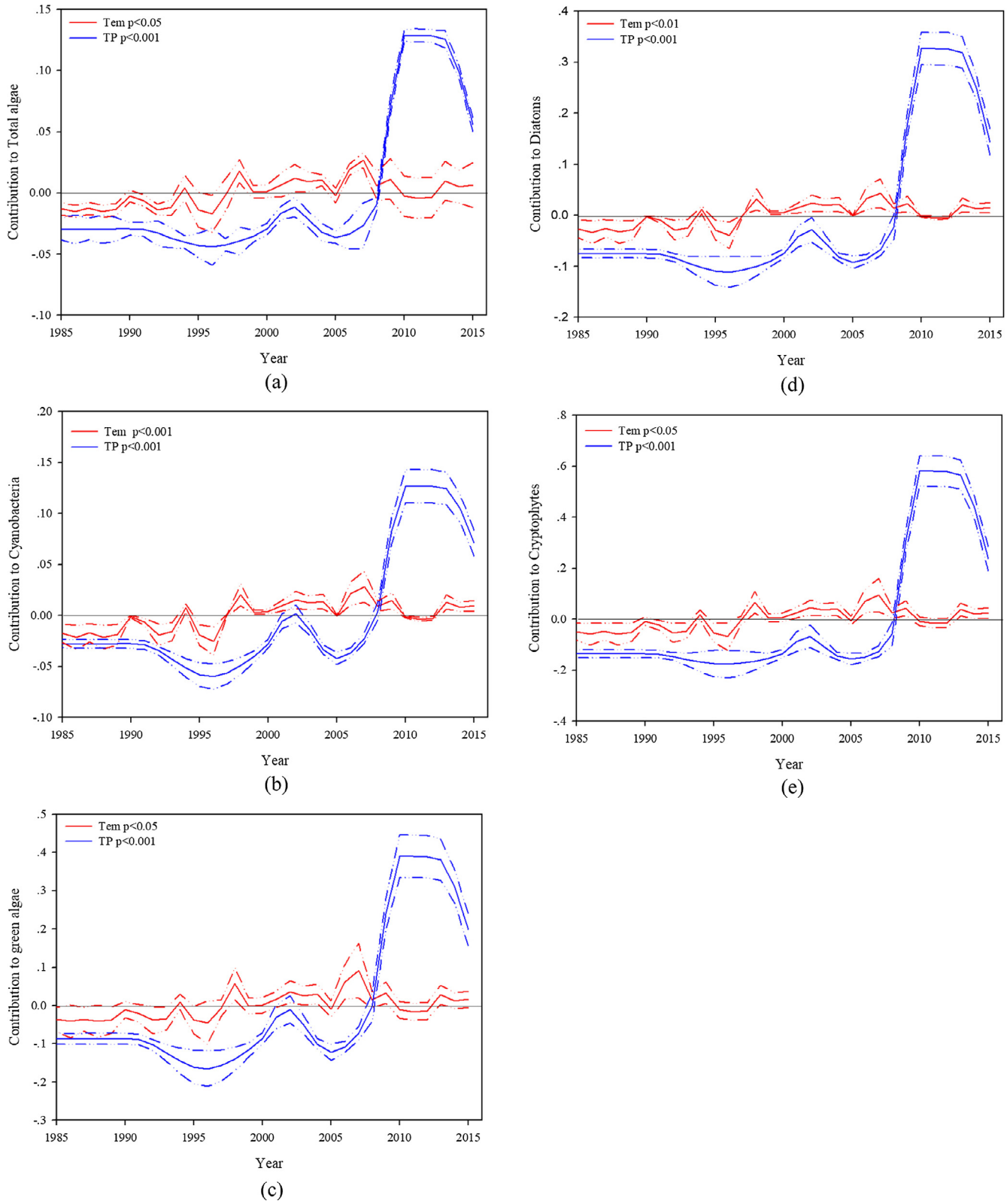

Fig. 5. GAM analysis results for the contribution of sedimentary TP (blue line) and annual average air temperature (red line) to the biomass variation of total algae (a), cyanobacteria (b), green algae (c), diatoms (d) and cryptophytes (e) in Reservoir Changtan. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

($n = 62$, $p < 0.01$; Table 1). Warming air temperature can heat the epilimnion, leading to stronger thermal stratification within lakes (Kraemer et al., 2015; Posch et al., 2012), which may impede water turnover and affect the compensation of hypolimnetic O_2 deficits (Yang et al., 2016). This can directly impact phytoplankton physiology (Posch et al., 2012), potentially leading to taxonomic shifts and biodiversity loss (O'Beirne et al., 2017).

Furthermore, the Changtan Reservoir, located in a subtropical

Table 2
GAMs analysis results for algae succession in Reservoir Changtan.

	Tem (%)	Sed-TP (%)	R^2	Dev.
Total algae (ββCar)	10.80	41.37	0.916	0.926
Cyanobacteria (Zea)	14.02	43.86	0.912	0.919
Green algae (Lut)	14.13	58.91	0.895	0.906
Diatoms (Diato)	25.64	97.36	0.944	0.950
Cryptophytes (Allo)	17.31	70.24	0.940	0.947

lowland region, is highly vulnerable to extreme weather events, particularly extreme high temperature (Havens et al., 2016). The phytoplankton biomass in the Changtan Reservoir experienced an unprecedented upsurge in 2007 (Fig. 2). This could be attributed to the extreme high temperature that triggered the multiplication of algae organisms due to sufficient nutrient levels (Havens et al., 2016; Posch et al., 2012).

Precipitation influences phytoplankton biomass dynamics due to greater runoff into water bodies (Toride et al., 2018; Zhou et al., 2016). Although no significant correlations were found between sedimentary pigments and precipitation (Table 1), indirect impacts of rainfall on phytoplankton biomass may have been neglected (Havens et al., 2016). Precipitation is plentiful in the study area; heavy rainfall may promote the formation of harmful algae blooms due to the re-suspension of benthic algae organisms and/or increases in primary productivity (O'Beirne et al., 2017; Yang et al., 2016). Low wind speed can also be a precondition for harmful algae bloom occurrence by affecting the synthesis of gas vesicles and distribution of algae cells (Helbling et al., 2015; Yang et al., 2016). The Changtan Reservoir is strongly influenced by a warm, moist air mass and typhoons in July, August, and September, which results in enhancing vertical mixing, have a negative influence on algae bloom formation (Kraemer et al., 2015). Overall, the impact mechanisms of meteorological factors on the phytoplankton community, including air temperature, precipitation, and wind speed, are complex, interrelated, and difficult to separate and quantify (Mwangi et al., 2016).

3.4. Relative contribution of predictors to the phytoplankton community

GAM analysis was applied to estimate how and when climate change and anthropogenic activities contributed to variations in phytoplankton biomass (Capo et al., 2017). The contribution of the two predictors, Sed-TP, and temperature, to the variation of total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass are shown in Fig. 5. Significant correlations ($p < 0.05$) were found between the response variables and explanatory variables in all models. The adjusted coefficients of determination (R^2) for the GAMs were all greater than 0.895, indicating good relationships between the explanatory variables and response variables. For all five models, the contribution of Sed-TP increased sharply and was much larger than that of temperature after around 2007. The negative effect of Sed-TP ($p < 0.001$) on response variables changed to a positive effect after 2007 (Fig. 5).

These changes were concurrent with a significant increase in algae biomass. The Changtan Reservoir experienced increasing inputs of N, P, and N: P ratio, and developed P-limiting conditions for phytoplankton, accelerating algae growth and promoting primary productivity in the reservoir, which was similar with the literatures (Posch et al., 2012; Zhou et al., 2016). The responses of total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass to temperature ($p < 0.05$) were positive since the late 1990s (Fig. 5). The increasing trend's turning point for temperature occurred in 1997 according to the M-K test (Fig. 4), consistent with the results above. GAM simulations indicated that a temperature upsurge would affect algae population dynamics positively, due to the enhanced growth rate, increased water column stability, and extended growing season (Visser et al., 2016).

The relative contribution of Sed-TP to variations in total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass (Table 2) suggested that TP was a good predictor of phytoplankton biomass. The relative contribution of temperature to variations in total algae, cyanobacteria, green algae, diatom, and cryptophyte biomass (Table 2) suggested that the response of phytoplankton biomass to temperature depends strongly on nutrient load, which was consistent with previous study (Visser et al., 2016). A previous study found that cyanobacteria biomass was influenced by nutrients and temperature, the nutrients explained a larger proportion of the variation according to data from more than 1000 lakes in the United States (Marieke et al., 2013). Research using data from 143 lakes along a latitudinal gradient from Europe to South America indicated that at lower nutrient levels, the frequency of cyanobacterial occurrence was below 30% over a wide

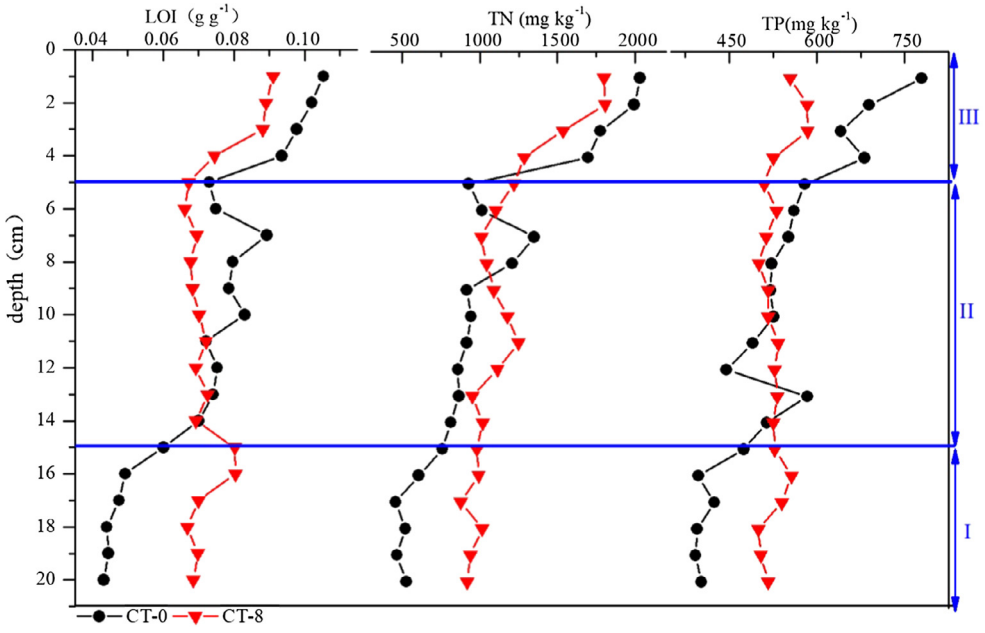

Fig. 6. Profiles of LOI, TN and TP from core samples CT-0 (a) and CT-8 (b).

range of water temperatures, rising very slowly; in contrast, at higher nutrient concentrations, there was a rapid and nonlinear increase in cyanobacterial biovolume with temperature (Havens and Paerl, 2015; Paerl and Otten, 2013). These results showed that the impact of temperature on phytoplankton biomass was slight at low nutrient levels, consistent with the current study. Moreover, the influence of nutrients and temperature varied among algae taxa (Rigosi et al., 2014). For instance, some taxa (such as *Anabaena*) responded more strongly to increasing nutrients than rising temperature, whereas other taxa (such as *Microcystis*) were more sensitive to rising temperature (Rigosi et al., 2014; Visser et al., 2016).

The GAMs explained the variance of diatoms best, with Sed-TP ($F = 212.65$, $p < 0.001$) accounting for 97.36% and temperature ($F = 9.12$, $p < 0.01$) accounting for 24.64% (Table 2). Diatoms have relatively high growth rates and are generally adapted to low light levels in high nutrient containing water compared with other algae taxa (Reynolds, 2006). Winder et al. (2009) found that smaller planktonic diatom species are suitable for living in increased nutrients and stratification conditions in Lake Tahoe, California for past decades. Moreover, the diatom assemblage structure can be influenced by confounding factors such as fluctuations in temperature, light intensity, discharge, and grazing pressure (Lavoie et al., 2014). Diatoms are sensitive to temperature, so lower temperatures can promote diatom growth because their optimal temperature for growth and photosynthesis is around 15 °C (Paerl and Otten, 2013). Considering the broad heterogeneity of morphological and eco-physiological traits among diatom species (Reynolds, 2006), the best adaption for diatoms to increasing nutrients and climate warming-induced mixing alterations may be species selection (Winder et al., 2009).

Increases in sediment TP concentration since 2007 have significantly raised the contribution of TP to algae biomass, seriously threatening the water quality of the Changtan Reservoir (Fig. 6). On the other hand, as climate change persists, the reservoir is likely to become dominated by cyanobacteria and experience algae blooms, even without a further rise in nutrient inputs. Our results imply that a climate-driven change in water temperature would modify the phytoplankton community toward those species favoring increased nutrients and higher water temperatures. The longer action to control eutrophication is delayed, and the more time that climate change is given to develop synergistic effects on nutrients, the less likely it becomes that eutrophication control will be achieved (Havens and Paerl, 2015). Hence, climate change should be considered within the context of evolving nutrient mitigation strategies for eutrophication control to maintain the water quality in watersheds such as the Changtan Reservoir.

With increasing urbanization, many climate change adaptation policies should be explored to mitigate nutrient loading into aquatic environments. For example, protection and restoration of buffer strips in stream systems provide an effective strategy to moderate temperature regimes and offset warming, and protect water quality for downstream ecosystems and water supply areas (Davies, 2010; Capon et al., 2013). Long-term management strategies must recognize and account for the fact that meteorological conditions are evolving as climate changes, impacting the path of nutrient inputs through watersheds and affecting nutrient loading in water bodies. Climate-induced impacts to hydrological and thermal regimes enhancing algal growth in reservoir systems can be offset through improved management of environmental flow releases from reservoirs (Arthington et al., 2010; Poff et al., 2010).

4. Conclusions

Well-preserved sedimentary pigments preserve evidence for changes in primary production over the past thirty years in the Changtan Reservoir, China. The dominant phytoplankton groups (determined by pigment analysis) were cyanobacteria, green algae, diatoms, and cryptophytes, consistent with recent observational results for plankton. Sedimentary pigments recorded a significant upsurge in phytoplankton biomass in the Changtan Reservoir after 2007. M-K statistical tests showed that this was linked to a significant increase in air temperature over the catchment and a disastrous cyanobacterial bloom that occurred in the middle and lower reaches of the Yangtze River basin in May 2007.

Increases in anthropogenic nutrients and changes in climate affected phytoplankton dynamics and algae biomass in the reservoir. GAM analysis demonstrated that nutrient loading explained a larger proportion of algae biomass variation than temperature. In addition, a significant increase in Sed-TP had a positive effect on algae biomass from 2007 onward. Of the species considered, variations in diatoms were best explained by GAM analysis, indicating that diatoms may be the best-adapted of the phytoplankton taxonomic groups to warming temperatures and increasing nutrients.

Conflict of interest

The authors declared that there is no conflict of interest.

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